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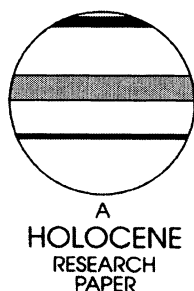
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Palaeolimnological and sedimentary responses to Holocene forest retreat in the Scandes Mountains, west-central Sweden

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Abstract: A suite of analyses was performed on sediments accumulated during the last 10 700 years in Lake Spåime, a small, hydrologically open water body in the modern alpine tundra zone of the Scandes Mountains, west-central Sweden. The study aimed to evaluate (1) the nature of climate changes that forced the late-Holocene lowering of altitudinal tree limit in the region, the timing of which is known from prior studies based on radiocarbon dating of subfossil wood, and (2) the impact of these vegetational changes on an aquatic ecosystem. Arboreal pollen and plant macrofossil data confirm the persistence of trees in the lake catchment at least from *c.* 9700 cal. BP until *c.* 3700 cal. BP. Although growing-season temperature is commonly believed to be the dominant factor driving boreal forest tree-limit variations in the region, a chironomid-based reconstruction of mean July air temperature suggests that local deforestation during the late Holocene was not accompanied by a significant cooling. The tree-limit retreat was more likely caused by increasing effective moisture and declining length of the growing season. The ecohydrological response of Lake Spåime to this combination of climate and vegetational changes included a decline in primary productivity, as indicated by an abrupt decrease in sediment organic matter content, while associated increases in organic $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and C/N point to diminished fluxes and altered balance of catchment-derived nutrients following deforestation. The decline in aquatic productivity is also marked by a distinct change in the mineral magnetic properties, from a high magnetic concentration assemblage dominated by fine-grained magnetite of biogenic origin to one dominated by background levels of coarse-grained detrital magnetite.

Key words: Holocene palaeoecology, alpine tree-limit dynamics, lake sediments, lacustrine nutrient cycling, stable isotope geochemistry, chironomidae, environmental magnetism, Sweden.

Introduction

Northern ecosystems are sensitive to global climate change and other environmental stresses, and are thus likely to be

particularly strongly affected by anthropogenically enhanced greenhouse warming (Cubasch *et al.*, 2001). Palaeoecological studies have provided numerous examples of past alteration of northern alpine and subarctic biomes related to variations in temperature and moisture regimes over a range of timescales during the Holocene epoch (e.g., Ritchie *et al.*,

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1983; MacDonald *et al.*, 1993; 2000; Kremenetski *et al.*, 1998; Barnekow, 2000; Wolfe *et al.*, 2000). Evidence exists for remarkably rapid vegetational changes even within the past hundred years apparently related mainly to increasing temperature, including an ascent of the alpine tree limit in Scandinavia of more than 100 m during the twentieth century (Kullman, 2001) and an expansion of shrub communities across areas of former tundra in parts of Alaska since the 1950s (Sturm *et al.*, 2001). Careful documentation of the nature and magnitude of such ecological changes is needed to assess the implications of ongoing and future climate change in the vast alpine and subarctic areas of northern Eurasia and North America, particularly with regard to carbon budgets (Oechel *et al.*, 1993).

The Scandes Mountains of Scandinavia form a suitable investigation area because of well-documented evidence for substantial past variation in the altitudinal limit of boreal forest, which was positioned as much as several hundreds of metres above the present-day tree limit during the early to mid-Holocene (e.g., Lundqvist, 1959; Karlén, 1976; Kullman, 1995). The western part of the Swedish province of Jämtland in the southern part of the Scandes stands out in this respect, due to extensive radiocarbon dating of subfossil wood remains (megafossils) of *Pinus sylvestris* L. (Scots pine), *Betula pubescens* ssp. *czerepanovii* (Orl.) Hämet-Ahti (mountain birch) and *Alnus incana* (L.) Moench (grey alder) encountered above present-day tree limits (Kullman, 1995; Kullman and Kjällgren, 2000). These datings suggest a long-term descent of the upper limit of boreal forest and a simultaneous expansion of alpine tundra ecosystems during the Holocene. Moreover, a well-defined altitudinal zonation was established during recent millennia, which gave rise to an intermediate subalpine zone of *Betula pubescens* that separates the alpine tundra from the predominantly coniferous boreal forest at lower altitudes.

Based on vegetational, geochemical, chironomid and mineral magnetic analyses of sediments in a small lake situated above the present-day tree limit, we reconstructed the response of a lake ecosystem in the Swedish Scandes to the climatically forced deforestation of its catchment during the late Holocene. This detailed multiproxy stratigraphic investigation allows us to establish the timing of local tree limit retreat, and to evaluate the temperature and moisture variations that forced this event and the resultant ecohydrological consequences. Prominent features included a reduction in aquatic productivity, probably related to decreases in the supply of dissolved inorganic carbon and nitrogen from catchment soils following forest retreat, as well as an associated decline in the authigenic formation of fine-grained magnetite.

Site description

Lake Spåime is located in the central part of the Scandes, west-central Sweden (63°07'N, 12°19'E), close to the drainage divide between the Baltic Sea and the North Atlantic Ocean (Figure 1). The lake is situated at 887 m a.s.l., c. 10 km north-east of the Sylarna Mountains, within an area underlain by Precambrian gneiss, mica-schist and amphibolite blanketed by hummocky till of Quaternary age. Deglaciation of the area occurred about 11 000–10 500 cal. BP (Lundqvist, 1998), leading to filling and draining of several generations of proglacial lakes dammed against the eastward-receding ice front at successively lower elevation (Borgström, 1989).

The catchment of the lake, which covers an area of c. 3.5 km², ranges c. 200 m in altitude along a gently sloping mountainside, facing east to northeast (Figure 1). The entire catchment is vegetated by alpine tundra, dominated by heath

communities with dwarf shrubs, willows, grasses, sedges and herbs. The modern-day forest limit of *Betula pubescens*, defined as the upper boundary of continuously distributed 2 m tall individuals, lies at c. 800 m a.s.l. in the area, penetrating into nearby valleys c. 5 km east and north of Lake Spåime. Scattered stands of tree-sized *Betula pubescens* also occur up to the local tree limit at c. 900 m a.s.l., although no specimens occur in the lake catchment at present. Predominantly coniferous boreal forest dominated by *Pinus sylvestris* and *Picea abies* (L.) Karst (Norway spruce) prevails at lower elevations, with tree-sized specimens of *Pinus sylvestris* reaching up to c. 720 m a.s.l. The vegetational zonation in the region and its relation to present and subrecent climates has been extensively studied by Kullman (1993a; 1998; 2001).

Lake Spåime is elongated (c. 400 m by 100 m; c. 0.03 km²) and has a maximum depth of c. 3.5 m. The lake is hydrologically open with its main inflow and outflow located at the southern and northern ends, respectively, as part of a well-developed stream system (Figure 2). The basin also receives some of its inflow from groundwater springs at the upslope (western) margin. Based on rough estimates of lake volume and discharge through the outlet stream, the residence time of the lake is estimated to be 5–10 days. Small lakes in the alpine zone of this region are generally ice-covered from mid-October to late May.

The climate in the region is characterized by a pronounced oceanic-continental gradient from northwest to southeast. Mean air temperatures for January and July range from –8°C to –11°C and from 10.5°C to 12°C, respectively, along this gradient, with mean annual air temperatures in the range of –1°C to 1°C and mean annual precipitation values between 900 and 500 mm, based on meteorological data collected during the period of 1961–90 at stations situated in valleys at 400–800 m a.s.l. (Alexandersson *et al.*, 1991). Mean annual and mean July air temperatures at Lake Spåime can be estimated to be –2 to –1°C and 9.4–10°C, respectively, based on sparse meteorological data from the area.

Methods

Fieldwork and subsampling

Multiple, overlapping sediment cores from staggered stratigraphic intervals were retrieved from the deepest, central part of the ice-covered lake in April 1999 at a water depth of 3.39 m, using a 7.5 cm diameter, 1 m long Russian peat sampler. The sediment profiles were extruded and described in the field, transferred to supportive liners, wrapped in plastic film and transported to cold storage (4°C). The 1 m long core segments were correlated in the laboratory based on measurement of magnetic susceptibility at 4 mm increments using a Bartington Instruments MS2E1 surface scanning sensor coupled to a Tamiscan-TS1 automatic logging conveyor. The 3.13 m thick sediment sequence was divided into 101 contiguous sections, 19–48 mm thick (generally c. 30 mm), and adjusted to lithostratigraphic boundaries. Subsamples of the contiguous sections were separated, respectively, for analyses of chironomids and elemental and stable isotope geochemistry. For mineral magnetic analyses, plastic boxes with an internal volume of 7 cm³ and a stratigraphic coverage of 19 mm were pushed into the sediments (centred at the midpoints of the 101 sections) and cut out with a nonmagnetic knife. The remaining parts of the contiguous sections were used for macrofossil analysis and radiocarbon dating. Samples for pollen analysis were collected at specific levels at 20–110 mm intervals (generally 90 mm) throughout the sediment profile. Samples of modern plants and soil profiles were collected in the immediate vicinity of the lake in December 2001.

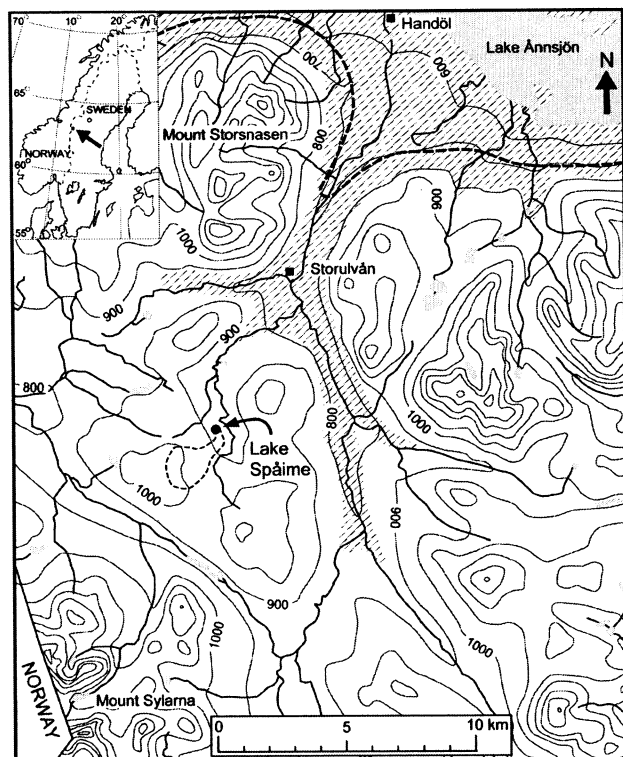


Figure 1 Map of the study area located in the Scandes Mountains, west-central Sweden (bold arrow on the inset map). The hatched area indicates the distribution of forest. Subalpine woodlands dominated by *Betula pubescens* form the altitudinal forest limit (c. 800 m a.s.l.) and scattered stands of *B. pubescens* extend to the tree limit (c. 900 m a.s.l.), whereas boreal forest with *Pinus sylvestris* and *Picea abies* occurs at lower elevations. The approximate altitudinal limit of tree-sized *Pinus sylvestris* (c. 720 m a.s.l.; Kullman, 1988) is marked by the heavy dashed line. The catchment of Lake Spåime is indicated by the thin dashed line.

Pollen and plant macrofossil analyses

Samples for pollen analysis from 36 levels (2 cm³) were prepared according to method A as described by Berglund and Ralska-Jasiewiczowa (1986). The samples were mounted in glycerol, and pollen grains were counted using a Leica DMLS light microscope at $\times 400$ and $\times 1000$ magnification. Plant taxonomy and identification of pollen and spores follow Moore *et al.* (1991). Comparisons were made with the pollen reference collection at the Department of Geology, Lund University. At least 500 tree pollen grains were counted at each level, except for a few of the lowermost samples where pollen concentrations were very low. In total, 48 pollen taxa and six spore taxa were identified, and pollen from trees, bushes, dwarf shrubs and herbs was included in the basic calculation sum. Pollen grains of *Betula* were treated as a single taxon, including both *B. nana* and *B. pubescens*.

For plant macrofossil analysis, fresh sediment samples, generally c. 50 cm³, were carefully washed through a 250 μ m sieve. Plant remains were collected from the sieve residue, determined and counted under a binocular microscope. The recorded abundances of fruits and needles of the respective taxa are expressed as numbers of individual plant fragments identified, whereas leaves, twigs and bark fragments are reported as presence or absence only, with the exception of *Empetrum* leaves.

Mineral magnetic analyses

Mineral magnetic analyses were undertaken on fresh sediment samples. Magnetic susceptibility (χ) was measured with a

Geofyzica Brno KLY-2 air-cored magnetic susceptibility bridge. Saturation isothermal remanent magnetization (SIRM) was induced at room temperature in a field of 1 T with a Redcliffe pulse-magnetizer (model 700 BSM), and the remanent magnetization subsequently measured with a Molspin Minispin magnetometer. After completion of the magnetic analyses, the samples were oven-dried at 40°C and weighed to permit the calculation of mass-specific SI units. The majority of the mineral magnetic data were reproduced by analysis of samples from overlapping core increments.

Elemental and stable isotope analyses

Small subsamples of the 101 core sections were homogenized, dried and ground to powder for determination of total organic carbon (TOC) content, based on temperature-controlled combustion in pure oxygen with subsequent detection of CO₂ by infrared absorption photometry in a Leco RC 412 Multiphase Carbon Determinator. The TOC data are expressed on a total dry weight basis as percentages of elemental carbon. Twenty sediment subsamples were taken for analysis of bulk organic carbon and nitrogen elemental and stable isotope geochemistry. The samples were acid-washed in 10% HCl to remove trace amounts of carbonates, rinsed with deionized water and freeze-dried. Coarse-grained detritus (> 500 μ m) was removed by sieving. The fine-grained fraction was analysed for carbon and nitrogen content and stable isotope composition (¹³C/¹²C and ¹⁵N/¹⁴N, respectively) using a Micromass Isochrom continuous flow mass-spectrometer equipped with an elemental analyser at the University of Waterloo-Environmental Isotope Laboratory (UW-EIL). Carbon/nitrogen ratios (C/N) based on these analyses are expressed as weight ratios. Carbon and nitrogen isotope compositions are reported in δ -notation; $\delta = [R_{\text{sample}}/R_{\text{std}} - 1] \times 1000$ where R signifies the ¹³C/¹²C and ¹⁵N/¹⁴N ratios in the samples and VPDB and AIR standards, respectively. Repeated analyses of several samples provided an estimate of the analytical uncertainty, ± 0.06 ‰ for $\delta^{13}\text{C}$ and ± 0.12 ‰ for $\delta^{15}\text{N}$.

Samples of terrestrial vegetation and soil were also analysed for bulk organic C and N content, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ at the UW-EIL. Vegetation samples were rinsed with deionized water, dried and ground using a Wiley mill. Dried bulk soil samples were analysed as well as fine and coarse fractions separated by a 500 μ m sieve.

Chironomid analysis

Sediment samples from 57 levels were sieved using a 100 μ m mesh, and chironomid larval head capsules were picked out at $\times 30$ – $\times 50$ magnification. All head capsules retrieved were transferred to pure alcohol and mounted in Canada balsam prior to microscopic identification. On average, 83 head capsules were sorted from each level and identified in accordance with Rieradevall and Brooks (2001), Sæther (1976) and Wiederholm (1983), in comparison with the chironomid reference collection at the Museum of Zoology, University of Bergen, and in comparison with the identifications from the modern calibration data set. Mean July air temperatures were inferred from the record of square-root transformed chironomid percentage data, using a transfer function calculated by weighted average-partial least squares regression (WA-PLS) (ter Braak and Juggins, 1993) from a calibration data set relating chironomid distribution from 153 Norwegian lakes to mean July air temperature (Brooks and Birks, 2000; 2001; unpublished data). Sample-specific prediction errors were estimated by Monte Carlo simulations (5000 cycles) (Birks, 1995). In order to extract signal from noise and to better visualize the

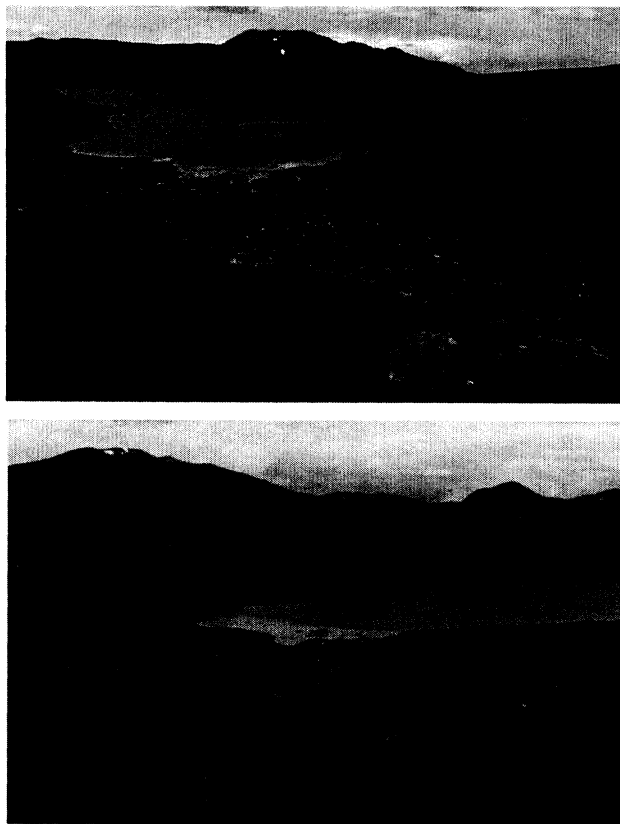


Figure 2 Photographs of Lake Spåime and the stream that runs through the lake (July 2000). Top: view towards north of the southern part of the lake and its main inlet. Bottom: view towards southeast of the northern part of the lake and its outlet.

temperature trends, a LOESS second-order smoother (Cleveland, 1993) with a span of 0.18 was run through all data points. Two approaches were used to evaluate the inferred temperatures. First, the percentages of total fossil assemblages that consist of taxa not represented in the calibration data were assessed. Secondly, analogue matching (Overpeck *et al.*, 1985), using squared chord distance as a measure of dissimilarity with 5% cut level for good analogues, was employed to assess how well the fossil assemblages were represented in the modern calibration data set. For both tests a 5% cut level was set to define any uncertain temperature estimate. The chironomid stratigraphy was divided into zones as assessed by sum-of-squares optimal partitioning criteria (Birks and Gordon, 1985), where the number of significant zones was determined by comparison with a broken-stick model (Bennett, 1996).

Comparison with independent vegetational data

The stratigraphic records obtained from the Lake Spåime sediment profile were compared to data sets of radiocarbon dated specimens of subfossil wood fragments (megafossils) encountered within the alpine tundra and the adjacent subalpine zone of *Betula pubescens* forest in the area. The megafossil data sets include 161 samples of *Pinus sylvestris* (Lundqvist, 1959; 1969; Kullman, 1980; 1987; 1988; 1989; 1995; Kullman and Kjällgren, 2000), 64 samples of *Betula pubescens* (Kullman, 1988; 1989; 1995) and 17 samples of *Alnus incana* (Kullman, 1988; 1995) collected above the modern altitudinal tree limits of the respective species. To provide a common calendar-year timescale for comparison of these data to the Lake Spåime records, the reported radiocarbon ages were converted to

calibrated ages based on the IntCal98 calibration data set (Stuiver *et al.*, 1998), using the OxCal 3.5 radiocarbon calibration software. The results are expressed as mid-intercepts or most probable intercepts with the calibration curve within 95.4% probability envelopes. For greater clarity, points rather than intervals were used to represent the calibrated ages. All three distributions of calibrated ages of the respective sets of subfossil wood samples were plotted against altitude in relation to the late nineteenth-century tree limit of *Pinus sylvestris* in the area (*c.* 680 m a.s.l. at Mount Storsnasen; see Figure 1). The material was collected within a continuous mountain area of *c.* 8000 km² (Kullman, 1995) with maximum distances of individual samples from Lake Spåime of *c.* 50 km.

Sediment description and chronology

The 3.13 m thick sediment sequence was classified into five lithostratigraphic units partly based on TOC content (Table 1). The lowermost 0.11 m thick part of the sequence (units 1–2) consists of silt followed by clayey and sandy silt with a gradual increase in TOC content (Figure 3). Following a 2 cm thick transitional layer of silty gyttja (unit 3), the sediments grade into a fairly uniform sequence of dark brown, slightly clayey gyttja. The lower, 1.4 m thick part of this sequence (unit 4), which contains occasional coarse organic detritus, exhibits a relatively high and variable TOC content (unit 4). The upper, 1.6 m thick part of the organic-rich sequence (unit 5) consists of slightly clayey gyttja with a rather constant and significantly lower TOC content as compared to the underlying units. The carbon analysis did not detect any carbonates or other inorganic carbon.

The chronology of the sediment sequence is based on eight calibrated AMS radiocarbon dates obtained on macroscopic remains of terrestrial plants (Table 2). Calendar-year ages expressed as 95.4% probability envelopes were obtained by calibration of the radiocarbon dates following the same procedure as for subfossil wood samples (see above). The age-depth model (Figure 3) was based on a five-degree polynomial adjusted to average values of the age ranges or mid-intercepts with the calibration curve for dates with irregular probability distributions. The sediment surface (3.39 m) was assumed to represent approximately present-day conditions (*c.* –50 cal. BP) although the water depth may have been slightly overestimated as a result of loose sediments near the surface. The lowermost radiocarbon date has a mid-intercept age of 10470 cal. BP, and the base of the sediment profile (0.025 m below the lowermost radiocarbon date) was tentatively assigned an age of 10700 cal. BP. This estimate, which represents a minimum age of the onset of sedimentation at Lake Spåime, is consistent with previous radiocarbon based datings of the deglaciation in the region (Lundqvist, 1969; 1998). As a probable result of differential sediment compaction, the apparent sediment accumulation rate changed successively from 0.11 mm year⁻¹ below *c.* 6.2 m to *c.* 0.40 mm year⁻¹ in the upper part of unit 4 and the lower part of unit 5, followed by values exceeding 0.50 mm year⁻¹ above *c.* 3.8 m.

Results

Pollen and plant macrofossil records

A summary pollen diagram along with selected pollen and plant macrofossil taxa indicative of major vegetational changes (i.e., the presence or absence of trees) are used to determine the

stratigraphic signature of the retreat of continuous forest from the catchment of Lake Spåime (Figure 4). With the exception of the initial 2000-year period, tree pollen frequencies generally decline throughout the profile with values of *c.* 82–95% at *c.* 9400–3500 cal. BP, 80–85% at *c.* 3400–1700 cal. BP and 65–77% at *c.* 1500 cal. BP to the present. Herb-pollen frequencies exhibit a corresponding upward-increasing trend from *c.* 5% to *c.* 25%, while shrubs and dwarf shrubs show largely uniform values, generally below the 1% and 5% levels, respectively. The pollen frequency records of *Pinus* and *Betula* show large variations in the ranges of 14–81% and 8–65%, respectively, although consistent and mutually opposite trends are clearly visible in most of the profile. Major changes towards lower *Pinus* pollen frequencies were centred at *c.* 7600, *c.* 3400 and *c.* 1600 cal. BP, whereas distinctly increasing values occur at *c.* 9500 and *c.* 600 cal. BP. *Alnus* pollen frequencies are generally stable at levels below 5% with the exception of an increase to 7–13% at *c.* 8000–6400 cal. BP. Further details of the pollen record from Lake Spåime were presented by Holmgren (2000).

Macrofossils of *Betula pubescens* were more frequently recorded in units 3 and 4 (*c.* 9700–3700 cal. BP) than in unit 5 (*c.* 3700–0 cal. BP), whereas the opposite pattern was observed for *Betula nana* and *Empetrum*. Small amounts of needles and bark fragments of *Pinus sylvestris* were recorded at *c.* 6500–5500 cal. BP. *Salix* macrofossils, mainly originating from dwarf willows, predominantly occur around 10 500, at *c.* 5400–3900 and after *c.* 2500 cal. BP. Full details of the plant macrofossil record from Lake Spåime were presented by Lamme (2000).

Elemental, mineral magnetic and stable isotope records

Following low and slowly rising values of TOC (*c.* 0.3–6%) prior to *c.* 9700 cal. BP, a rapid increase to *c.* 15% was recorded, with subsequent variations in the range of 8–19% between 9700 and 3700 cal. BP (Figure 5). The later part of the Holocene is characterized by significantly lower variation in TOC content, exhibiting values in the range of 6–10% following a distinct decrease at *c.* 3700 cal. BP. The elevated TOC content of unit 4 (*c.* 9500–3700 cal. BP) correlates with relatively high values of TN (*c.* 0.7–1.5%) while lower and more stable TN values (*c.* 0.4–0.6%) were recorded after *c.* 3700 cal. BP. The records of χ and SIRM exhibit elevated values prior to *c.* 3500 cal. BP, showing clear patterns of covariance with TOC (and TN) content, including peaks at *c.* 8700, 7300, 6200, 5300 and 4400 cal. BP, and corresponding low values at *c.* 8000, 5900 and 4800 cal. BP. These apparent relationships are illustrated by the positive correlation between TOC content and SIRM within unit 4 (*c.* 9500–3700 cal. BP; Figure 6). In contrast, no such correlation is detectable in unit 5 (*c.* 3700–0 cal. BP), which is

characterized by low and slowly declining values of χ and SIRM. SIRM/ χ ratios predominantly in the range of 20–35 10^{-3}Am^{-1} were recorded prior to *c.* 4800 cal. BP, followed by lower values, gradually declining to *c.* 10 10^{-3}Am^{-1} in the younger part of the record.

Relatively low C/N ratios (*c.* 10–13) were recorded before *c.* 3200 cal. BP, followed by higher values (*c.* 14.5–15) during the subsequent part of the Holocene, except for the sample near the top of the core, which gave a C/N ratio near 13 (Figure 5). Bulk organic $\delta^{13}\text{C}$ values in the range of –29 to –28‰ were recorded before *c.* 6300 cal. BP, followed by rather constant values around –27.5‰ throughout the rest of the core. Bulk organic $\delta^{15}\text{N}$ values generally range between –0.2 and +0.5‰ prior to *c.* 2700 cal. BP, followed by a slight enrichment in ^{15}N to maximum values (*c.* +0.6 to +0.9‰). The uppermost sample exhibits a $\delta^{15}\text{N}$ value of *c.* –0.3‰.

Elemental and stable isotope data obtained on modern soil and vegetation

Samples of modern plant material from the immediate vicinity of the lake yielded TOC and TN values in the ranges of 44–69% and 0.6–1.2%, respectively, resulting in C/N ratios between 50 and 114 (Table 3). Two soil samples from the catchment with mutually different contents of organic material showed C/N ratios ranging from 36 to 39 as obtained on bulk samples and two different particle-size fractions. Minor inorganic N content of the partly minerogenic soil samples was corrected for, using the simple TOC-TN crossplot test proposed by Talbot (2001). Bulk organic $\delta^{13}\text{C}$ values of the soil and vegetation samples were between *c.* –28.5‰ and *c.* –25.8‰, whereas corresponding $\delta^{15}\text{N}$ values range from *c.* –4‰ to *c.* –0.4‰ with the majority of values below –2‰. No significant differences in $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ were observed between fine and coarse fractions of soil samples (Table 3).

Chironomid stratigraphy and inferred temperature reconstruction

In total, 82 chironomid taxa were identified, of which 12 were recorded with more than 100 occurrences. Figure 7 shows a selection of the most important components of the chironomid stratigraphy, as well as the division into four zones based on significant faunal changes at *c.* 8500, 3600 and 2300 cal. BP. A more detailed account of the chironomid record will be presented elsewhere.

Analogue matching revealed that the species assemblages of the two lowermost of the 57 core samples examined are poorly represented in the modern calibration data set, although no samples exhibit assemblages with more than 5% of taxa not present in the modern calibration data set. As shown in Figure

Table 1 Lithostratigraphic description of the Lake Spåime sediment profile (depths are related to the water surface)

Unit	Depth (m)	Description	TOC content (%)
5	3.39–5.01	Dark brown, slightly clayey gyttja. Lower boundary very gradual. Moss remains at 3.56–3.59 m.	6.44–9.80
4	5.01–6.39	Dark brown, slightly clayey gyttja with occasional occurrences of coarse organic detritus. Abundant moss remains at 5.24–5.32 m. Lower boundary gradual.	7.80–18.70
3	6.39–6.41	Dark brown silty gyttja. Lower boundary gradual.	5.69
2	6.41–6.50	Grey slightly organic silt with layers of clay and sand. Lower boundary gradual.	0.67–1.98
1	6.50–6.52	Grey clayey silt. Abrupt core stop at 6.52 m.	0.30

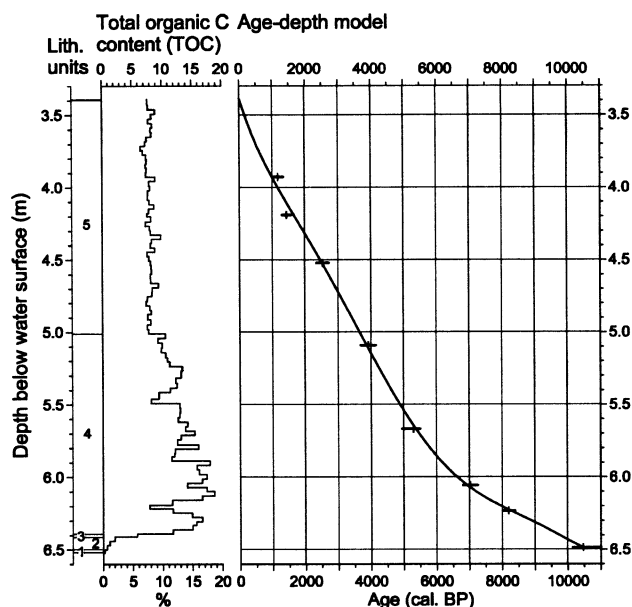


Figure 3 Age-depth model based on calibrated radiocarbon dates of terrestrial macrofossils (Table 2), along with the lithostratigraphic subdivision of the Lake Spåime sediment profile (Table 1) and the record of total organic carbon content (TOC).

4, the sample specific error estimates of the chironomid-inferred reconstruction of mean July air temperature range from 1.0 to 1.2°C. Subsequent to smoothing, the temperature reconstruction exhibits a cooling of *c.* 2°C from the earliest part of the Holocene to the present. Shortly following deglaciation, mean July air temperatures were close to 11.5°C. Temperatures decreased steadily from this point, reaching a minimum of *c.* 9.4°C around 8300 cal. BP, followed by a general temperature increase which peaked at *c.* 10.5°C around 5600 cal. BP. A subsequent cooling led to persistently lower average temperatures (*c.* 9.6°C) between *c.* 4800 and 2600 cal. BP. The inferred temperature increased from *c.* 2600 cal. BP to *c.* 2100 cal. BP, attaining a peak of *c.* 10.0°C. This was succeeded by a progressive cooling from 2000 cal. BP to the present, punctuated by a transient rise around 1000 cal. BP to *c.* 9.9°C, and a slight increase following the Holocene minimum of 8.9°C at *c.* 350 cal. BP. The inferred temperature at the top sample (9.3°C) is close to the present estimated mean July temperature at the site (9.4–10.0°C). The temperature reconstruction for the last 4000 years is characterized by higher variability than earlier parts of the Holocene.

Interpretation and discussion

The forest retreat at Lake Spåime

Based on major patterns, the pollen and plant macrofossil records can be divided into two main zones (Figure 4), the intervening boundary of which broadly coincides with the lithological transition from unit 4 to unit 5 (*c.* 3700 cal. BP). Relatively high frequencies of *Betula pubescens* fruits in the lower part of the record provide strong evidence for the local presence of this species from *c.* 9700 cal. BP. *Betula* pollen frequencies are also higher than at present before *c.* 5000 cal. BP, except for a period around 8500 cal. BP. Needles and bark fragments in the sediments indicate that *Pinus sylvestris* also grew at the site, at least between 6500 and 5500 cal. BP, a period of relatively high chironomid-inferred temperatures. After *c.* 3800 cal. BP, *B. pubescens* fruits are less abundant and occur more erratically. This change indicates a lowering of the forest limit and most probably a transition from boreal forest to sub-alpine woodland tundra characterized by scattered stands of *B. pubescens* (Sjörs, 1963). The increase in *Pinus* pollen frequency to a peak shortly after this transition may therefore reflect successively increased openness of forests in the area, causing enhanced deposition of wind-blown pollen from nearby forested valleys, rather than increased abundance of *P. sylvestris* near the lake. In general, the total tree-pollen record shows stable and relatively high frequencies until *c.* 3500 cal. BP, when decreasing tree-pollen and elevated herb-pollen frequencies were recorded, also indicative of forest retreat. Subsequent to this shift, the catchment vegetation was probably dominated by heath components, as indicated by the increased macrofossil abundance of *Betula nana* and *Empetrum*, and to some extent also *Salix*. Thus, it can be assumed that the general change in macrofossil content between 4000 and 3500 cal. BP represents the disappearance of continuous forest from the lake catchment.

The distinct lowering of *Pinus* pollen frequencies at *c.* 1600 cal. BP indicates a retraction of boreal forest also from nearby valleys. Herb-pollen frequencies increase substantially, reaching values comparable to treeless sites in similar settings in the Scandes (Barnekow, 1999). The most recent 600-year period is marked by decreasing *Betula* pollen frequencies to present-day values, a related increase in *Pinus* pollen values and absence of *B. pubescens* macrofossils. These changes probably reflect the retreat of *B. pubescens* forest from nearby valleys, and the ultimate disappearance of scattered trees in the catchment of Lake Spåime, respectively.

The compilation of published radiocarbon dated findings of subfossil wood can be used as an additional, independent proxy for long-term Holocene vegetational change in the area surrounding Lake Spåime. As evidenced by the megafossil

Table 2 Radiocarbon dates

Sample depth (m)	Lab. no.	Material analysed*	Weight (mg)	$\delta^{13}\text{C}$ (‰ VPDB)	Reported age (^{14}C years BP)	Calibrated age (2 σ interval)	Calibrated age (mid intercept)
3.90–3.96	Ua-16679	<i>Bet.</i> , <i>Sal.</i>	> 5**	-26.4	1295 \pm 75	1010–1340	1175 cal. BP
4.18–4.20	Ua-16678	<i>Bet.</i> , <i>Sal.</i>	< 3**	-25.0***	1555 \pm 65	1300–1570	1435 cal. BP
4.51–4.54	Ua-16680	<i>Bet.</i> , <i>Sal.</i>	> 5**	-27.4	2420 \pm 65	2340–2720	2530 cal. BP
5.07–5.11	Ua-16392	<i>Bet.</i> , <i>Emp.</i>	4.2	-27.2	3620 \pm 80	3690–4150	3920 cal. BP
5.65–5.68	Ua-16391	<i>Bet.</i> , <i>Sal.</i>	3.1	-28.0***	4580 \pm 70	4950–5500	5290 cal. BP
6.04–6.07	Ua-16390	<i>Bet.</i> , <i>Emp.</i>	23.2	-28.5	6165 \pm 75	6800–7250	7025 cal. BP
6.22–6.25	Ua-16389	<i>Bet.</i> , <i>Car.</i>	24.4	-28.5	7395 \pm 95	8010–8380	8195 cal. BP
6.47–6.50	Ua-16388	<i>Sal.</i>	3.1	-30.5	9315 \pm 160	10150–11000	10470 cal. BP

* *Bet.* = fruits, catkin scales, leaves and small twigs of *Betula pubescens*; *Sal.* = fruits, catkin scales, leaves and small twigs of *Salix* spp.; *Emp.* = seeds of *Empetrum nigrum*; *Car.* = fruits of *Carex* sp. All samples also included unidentified terrestrial leaf fragments.

** Exact sample weight not determined.

*** Assumed values ($\delta^{13}\text{C}$ not determined).

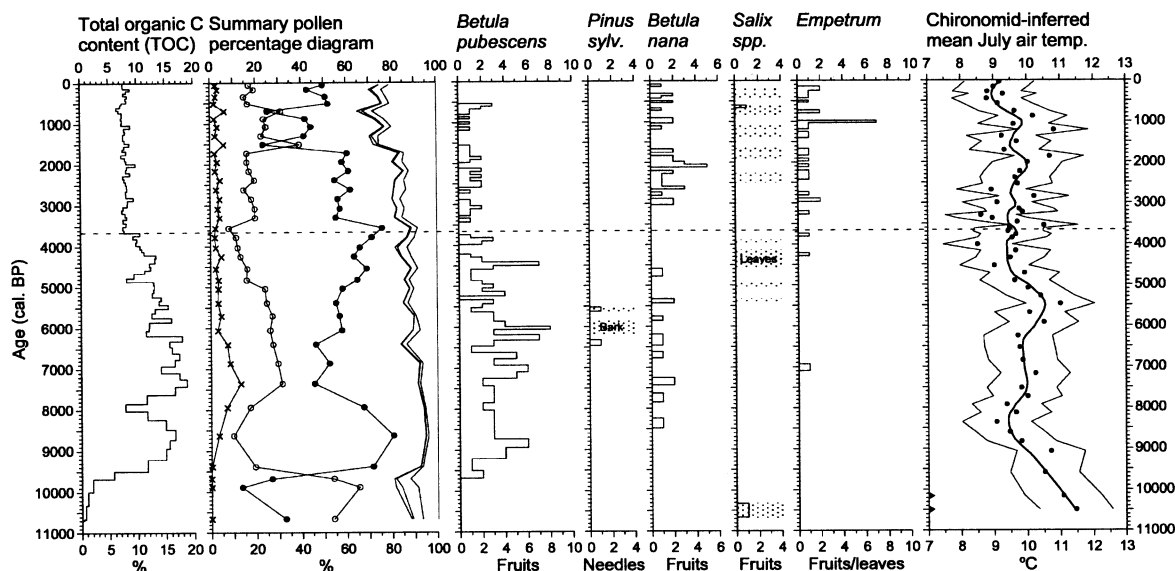


Figure 4 Selected pollen and plant macrofossil data from Lake Spåime, plotted against calendar-year age, showing evidence of the local retreat of continuous forest (dashed horizontal line). The summary pollen diagram is divided by solid lines into pollen percentages of trees, shrubs, dwarf shrubs and herbs (from left to right; 100% in total), with superimposed records of *Pinus* (filled circles), *Betula* including *B. nana* (open circles) and *Alnus* (crosses). The shaded zones in the panels of *Pinus sylvestris* and *Salix* spp. macrofossil data indicate the presence of bark and leaves and/or twigs, respectively, of these taxa. The record of total organic carbon content (TOC) and the chironomid-inferred reconstruction of mean July air temperature from the same core are shown for comparison. The thick line represents a LOESS smoothing of temperature determinations obtained on individual samples (filled circles), and sample-specific errors are indicated by marginal envelopes. The inferred temperature record has not been adjusted for glacio-isostatic land uplift. Samples exhibiting nonanalogue chironomid assemblages are indicated by arrows in the left-hand margin.

records available from the modern zone of *Betula pubescens* and the adjacent, presently treeless mountain areas (see Figure 1), tree-sized individuals of *P. sylvestris*, *B. pubescens* and *Alnus incana* were abundant at altitudes above their modern tree limits during most of the Holocene (Figure 8). The *P. sylvestris* megafossil record, which represents the most extensive data set, shows a consistent tree-limit descent during the last 11 000 years (Kullman and Kjällgren, 2000). It should be noted

that the rate of tree-limit retreat is slightly exaggerated prior to c. 9000 cal. BP due to the additional cooling with time brought about by the strong isostatic recovery subsequent to deglaciation. The megafossil data suggest that the tree limit of *P. sylvestris* was situated at about the altitude of Lake Spåime (c. 900 m a.s.l.) at c. 7000–5000 cal. BP, consistent with macrofossil evidence at the site at this stage (Figure 4). The local presence of *P. sylvestris* at even higher altitudes, in

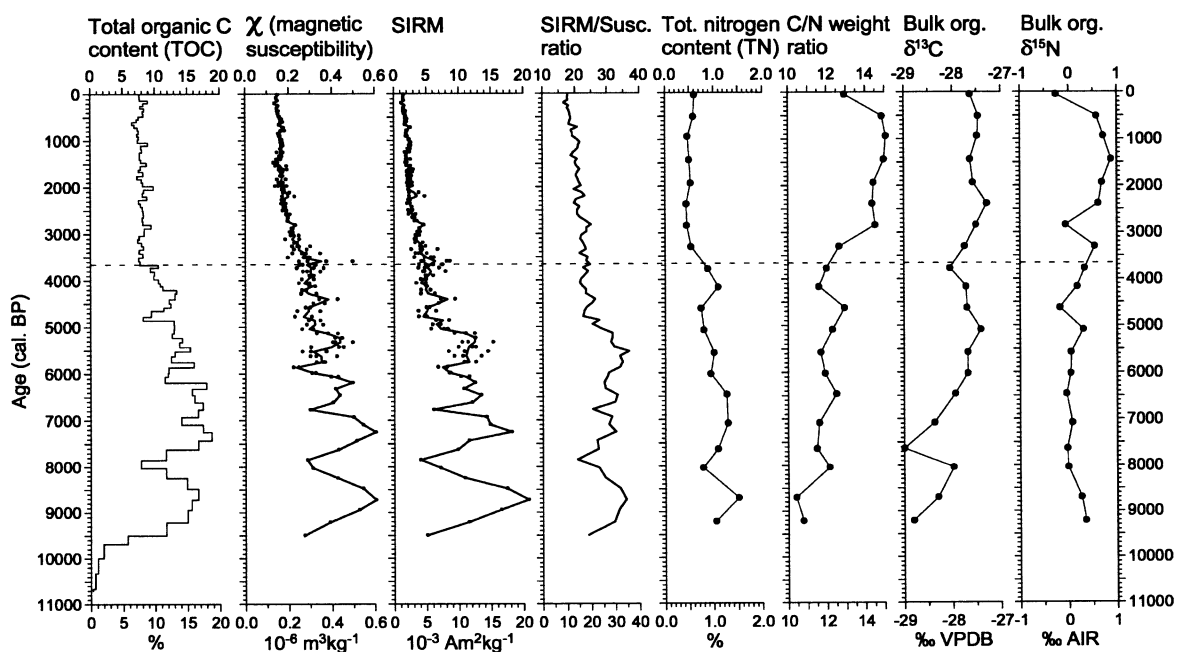


Figure 5 Records of total organic carbon content (TOC), mineral magnetic parameters, total nitrogen content (TN), elemental C/N ratio, and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of bulk organic material from the Lake Spåime sediment profile, plotted against a calendar-year age scale. The dashed horizontal line marks the inferred retreat of continuous forest from the lake catchment (see Figure 4).

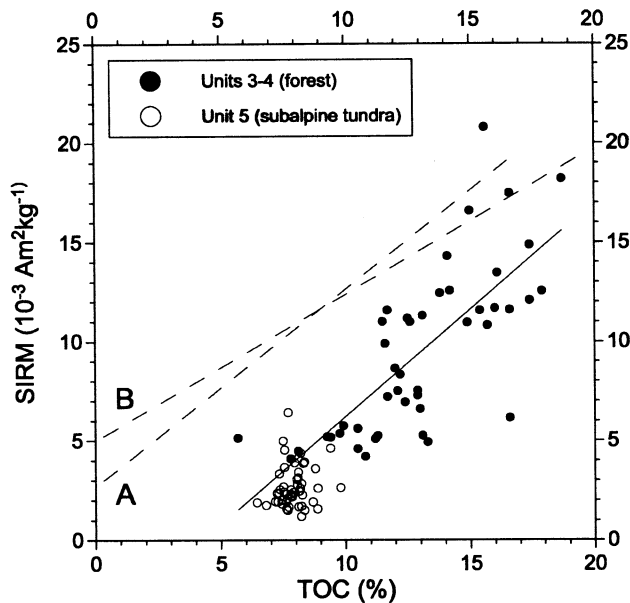


Figure 6 Crossplot of total organic carbon (TOC) content versus SIRM showing a positive linear relationship (solid regression line with a slope of 1.08; $r = 0.74$) between the two parameters for sediments deposited during the forest phase. The dashed lines represent the slopes of the regression equations obtained for identical parameters measured on Holocene varved sediment sequences in Lake Sarsjön (A) and Lake Frängsjön (B), which are located in an area of coniferous forest *c.* 400 km northeast of Lake Spåime (Snowball *et al.*, 2002).

good agreement with the megafossil data, has been stratigraphically confirmed by macrofossils encountered in lake sediments dating to *c.* 9200–8200 cal. BP at a nearby site, 100 m above Lake Spåime (*c.* 320 m above the late nineteenth-century tree limit of the species; J. Bergman, unpublished data), consistent with high pollen frequencies of *Pinus* at this stage.

As indicated by the concentration of *B. pubescens* megafossils at high elevations at *c.* 7500–5000 cal. BP, this species successively replaced *P. sylvestris* as the dominant tree-limit component, extending in altitude to at least 100 m above Lake Spåime. This development reflects the establishment of a subalpine zone of predominantly *B. pubescens* in the Scandes, probably as a result of declining seasonality (Kullman, 1992). During the *B. pubescens* expansion phase, *A. incana* was also part of the subalpine forest vegetation in the area,

as suggested by the well-defined group of megafossils in the range of *c.* 8300–5800 cal. BP, recovered at roughly the same or slightly higher altitudes as compared to the uppermost finds of *P. sylvestris*. The presence of *A. incana* in the vicinity of Lake Spåime at this stage is also indicated by elevated pollen frequencies of *Alnus* (Figure 4).

No megafossils younger than *c.* 4800 cal. BP have been recorded at altitudes exceeding *c.* 820 m a.s.l. (*c.* 140 m above the late nineteenth-century tree limit of *P. sylvestris*), with the exception of a single highly anomalous specimen of *B. pubescens* (Figure 8), which probably reflects the occurrence of scattered trees at sites with extremely favourable microclimates and soil conditions. This pattern of megafossil data clearly supports the inferences from the stratigraphic data presented here, i.e., that the catchment of Lake Spåime and other areas at about the same altitude have been continually occupied by subalpine woodland tundra or alpine tundra ecosystems at least during the last 3–4 millennia. The general Holocene tree-limit retreat is well documented and consistent with similar, though less detailed, megafossil records from other parts of the Scandes (Kullman, 1993b; Kvamme, 1993; Eronen and Huttunen, 1993) and with pollen stratigraphic data from Jotunheimen, south central Norway (Barnett *et al.*, 2001). However, it should be noted that, despite the extensive megafossil data sets collected during recent decades in Western Jämtland, the absolute altitudinal position of the tree limit at any given time must be considered as a minimum value based on the uppermost occurrence of subfossil specimens (Kullman and Kjällgren, 2000). Periodic absence of dated wood remains, which produces gaps in the data set along the long-term recessional trend, e.g., at *c.* 2000 cal. BP (Figure 8), does not provide unambiguous evidence of temporary tree-limit retreat and readvance.

Based on the independent lines of evidence for forest retreat provided by the stratigraphic changes and the megafossil data, respectively, it can be concluded that the retraction of continuous forest from the immediate vicinity of Lake Spåime is reflected by the distinct decrease in TOC content at *c.* 3700 cal. BP (Figures 4 and 8). The slightly delayed increase in herb-pollen frequencies in relation to this event probably reflects the relatively slow retreat of forest from the wide upland valley at altitudes less than 50 m below the site (Figure 1). Sediment TOC content and tree macrofossil frequencies (i.e., fruits of *B. pubescens*; Figure 4) exhibit broadly coherent trends, which suggests that TOC content may be indirectly related to forest density prior to deforestation of the site. Further support for this

Table 3 Bulk organic carbon and nitrogen elemental content and stable isotope composition of soil and vegetation samples collected in the catchment of Lake Spåime. Corrected C/N ratios for soil analyses account for estimated inorganic N fraction, as determined by a simple TOC-TN crossplot test (cf. Talbot, 2001)

Material analysed	TOC (%)	TN (%)	C/N ratio	C/N ratio (corrected)	$\delta^{13}\text{C}$ (‰ VPDB)	$\delta^{15}\text{N}$ (‰ AIR)
<i>Betula nana</i> wood	51.57	0.61	85.10		-26.85	-2.18
<i>Betula nana</i> bark	68.64	0.60	114.02		-27.87	-0.58
<i>Betula nana</i> bulk sample	59.05	1.16	50.77		-27.94	-0.40
<i>Empetrum nigrum</i> leaves	59.28	0.99	60.19		-27.96	-3.08
<i>Empetrum nigrum</i> wood	59.60	0.61	97.07		-28.20	-1.55
<i>Empetrum nigrum</i> bulk sample	58.04	0.78	74.70		-28.08	-3.53
<i>Vaccinium myrtillus</i> bulk sample	59.07	0.72	81.58		-28.47	-3.73
Unidentified lichens	44.64	0.67	66.43		-25.87	-3.32
Soil sample 1: bulk sample	42.04	1.27	33.19	37.20	-27.32	-2.76
Soil sample 1: < 500 μm	27.17	0.89	30.56	36.11	-26.32	-2.04
Soil sample 1: > 500 μm	43.04	1.26	34.10	38.24	-26.55	-2.77
Soil sample 2: bulk sample	24.82	0.80	31.14	37.58	-27.15	-3.36
Soil sample 2: < 500 μm	17.82	0.60	29.91	38.80	-26.78	-3.08
Soil sample 2: > 500 μm	32.05	0.96	33.29	38.79	-27.24	-3.91

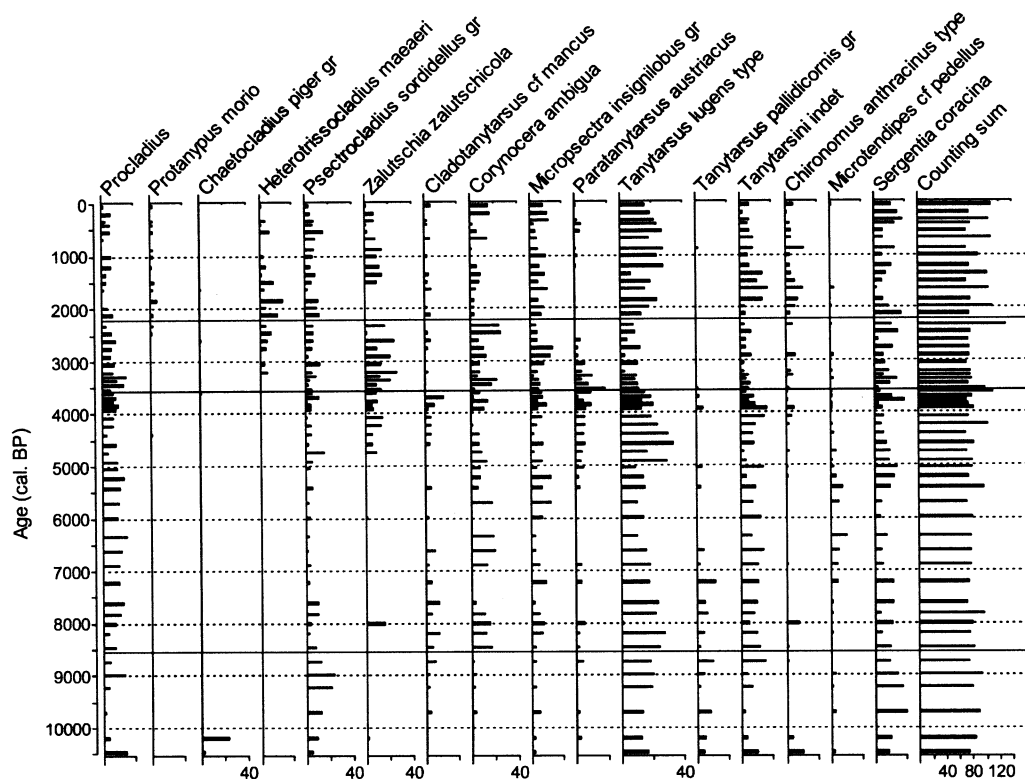


Figure 7 Selected chironomid taxa from the Lake Späime sediment profile, expressed as percentages of the total number of determinable head capsules. Solid lines represent statistically significant changes in the chironomid assemblage as determined by sum-of-squares optimal partitioning.

hypothesis is provided by the general covariance between TOC content and the temporal distribution of tree megafossils recovered above the late nineteenth-century tree limit of *P. c sylvestris* (Figure 8). Below we explore processes that may be responsible for the relationship between sediment TOC content and ecological variables, including changes in catchment vegetation and the limnic environment, using the lake sediment elemental and isotopic records.

Elemental and mineral magnetic stratigraphy and origin of sediment organic matter

As shown in Figure 5, the decrease in TOC content recorded at *c.* 3700 cal. BP, which is assumed to reflect deforestation of the lake catchment, is accompanied by distinct changes in several other parameters. In general, elevated mineral magnetic concentration parameters (χ and SIRM) during the forest episode correlate positively with TOC content as demonstrated in Figure 6. Together with distinctly higher SIRM/ χ ratios, these data suggest that fine-grained ferrimagnetic minerals are associated with organic matter produced *in situ* by magnetotactic bacteria, consistent with evidence from multiple studies of varved lake sediments in Sweden (Snowball *et al.*, 2002). Thus, the elevated mineral magnetic concentrations, which are not related to erosion, transportation and deposition of mineral matter, reflect a predominantly aquatic origin of the organic matter. Temporary reductions in magnetic concentrations during the forest episode, for example that centred at *c.* 8000 cal. BP, were most likely caused by lowered aquatic productivity. Between *c.* 5200 and *c.* 3700 cal. BP the positive relationship between mineral magnetic concentrations and TOC content breaks down, and the magnetic properties of the sediments that accumulated after *c.* 3700 cal. BP indicate dominance of relatively coarse-grained ferrimagnetic minerals at low concentrations, most likely detrital magnetite originating from a primary bedrock source. It should also be noted that the apparent

decline in TOC content and aquatic productivity at *c.* 3700 cal. BP is unlikely to be related to a general decrease in lakewater temperature, as suggested by the absence of any significant shift in chironomid-inferred mean July air temperature across this boundary (Figure 4).

The major shift in nutrient cycling of the lake indicated by the changes in TOC content and mineral magnetic data at *c.* 3700 cal. BP is also reflected by changing TN content, C/N ratios and bulk organic $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of the sediments at about the same time (Figure 5). Although the TN record exhibits broadly consistent long-term trends as compared to TOC, elemental C/N ratios, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ increase following the forest retreat. The increase in elemental C/N ratio to values around 15 could be reflective of an increase in the supply of terrestrial organic matter to Lake Späime in response to increased soil erosion following deforestation, as such material typically exhibits C/N ratios exceeding 20, as compared to aquatic plants which normally yield C/N ratios around 10 (Meyers and Lallier-Vergès, 1999). This type of relationship between catchment vegetation and C/N ratio of lake sediments has been observed in other boreal and subarctic areas. For example, Kaushal and Binford (1999) recorded an increase in C/N ratio and a decrease in organic matter content in response to historical deforestation in Massachusetts, and an early-Holocene expansion of alder shrub vegetation across former areas of birch tundra in Alaska was accompanied by decreased C/N ratio and increased total carbon content (Hu *et al.*, 2001). C/N ratios measured on modern soil samples and terrestrial vegetation in the catchment of Lake Späime are indeed high, with values ranging from 36 to 114 (Table 3), broadly consistent with data obtained on modern leaves from sites further north in the Scandes Mountains (Rundgren *et al.*, 2003). However, comparison of the sediment C/N and $\delta^{15}\text{N}$ records with the modern soil and vegetation data clearly indicates that the stratigraphic shift to higher values in both of

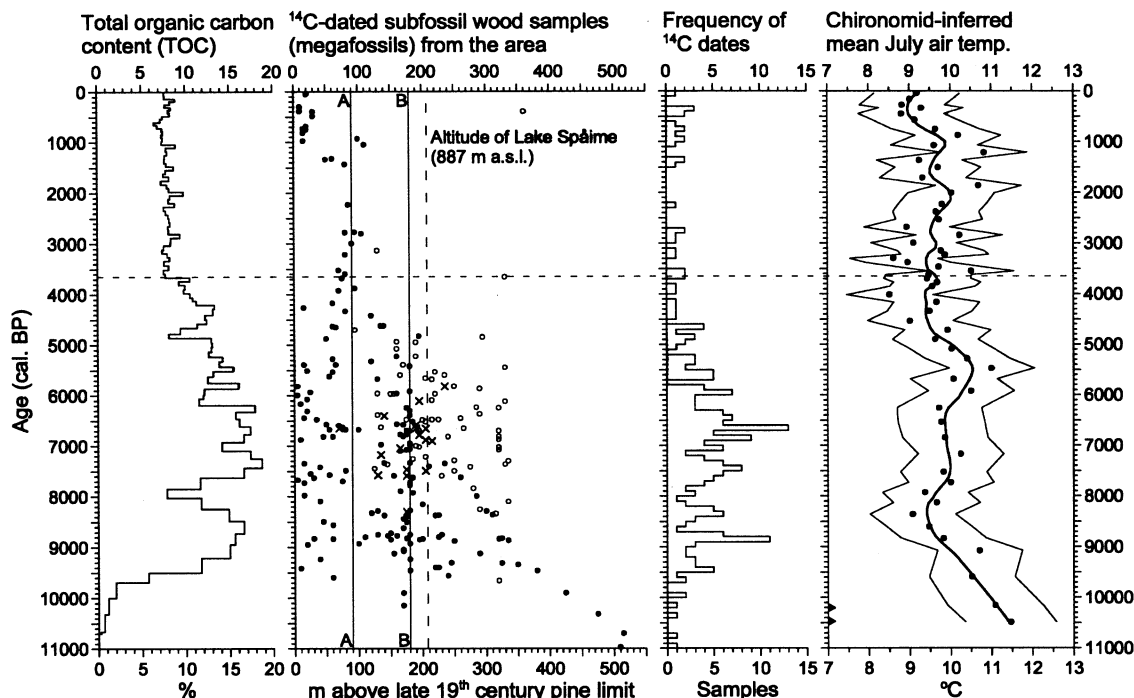


Figure 8 Published radiocarbon dated finds of subfossil wood (megafossils) from the area (see text for details) plotted against a calendar-year age scale. The approximate tree-limit altitude of *Pinus sylvestris* at the end of the nineteenth century (c. 680 m a.s.l. in the vicinity of Lake Spåime) was used as a reference level. Filled circles = *Pinus sylvestris*; open circles = *Betula pubescens*; crosses = *Alnus incana*. Temporal variations in the total number of radiocarbon dates of these three species are shown as a frequency histogram. The vertical lines (labelled A and B) represent the present-day tree limits in the area of *Alnus incana* and *Betula pubescens* ssp. *czerepanovii*, respectively. The dashed horizontal line marks the retreat of continuous forest from the lake catchment as inferred from stratigraphic data (Figure 4). The chironomid-inferred reconstruction of mean July air temperature and the record of total organic carbon content (TOC) from Lake Spåime are shown for comparison.

these parameters following deforestation is unlikely to be primarily due to inwash of organic soil detritus or remains of terrestrial vegetation as these components exhibit $\delta^{15}\text{N}$ values below 0‰ (Figure 9). As elaborated below, the decrease in TOC content and the shift in carbon and nitrogen stable isotope composition observed at c. 3700 cal. BP may alternatively reflect a response of lakewater nutrient balance to changes in catchment vegetation and nutrient supply. The anomalously low C/N ratio (and associated depletion in ^{15}N) recorded in the most recent sample is probably related to preservation of labile nitrogen in the uppermost sediments prior to diagenetic effects (cf. Wolfe *et al.*, 1999).

Carbon and nitrogen stable isotope stratigraphy

The carbon isotope composition of lake sediment organic matter ($\delta^{13}\text{C}_{\text{org}}$) may reflect a variety of environmental factors (Håkansson, 1985; McKenzie, 1985; Hammarlund, 1993). The $\delta^{13}\text{C}$ signature of autochthonous organic matter specifically may largely depend on the $\delta^{13}\text{C}$ of dissolved inorganic carbon (DIC) in lake water. The $\delta^{13}\text{C}$ of DIC may, in turn, be influenced by isotopic exchange with atmospheric CO_2 (Turner *et al.*, 1983; Talbot, 1990) and productivity-driven ^{13}C -enrichment due to preferential uptake of ^{12}C by phytoplankton during photosynthesis (Meyers, 1993; Brenner *et al.*, 1999). Both of these processes tend to increase the $\delta^{13}\text{C}$ of DIC, while recycling of ^{13}C -depleted carbon from soil respiration and decay of organic matter in the water-column and bottom sediments is a process that generally leads to lower $\delta^{13}\text{C}$ of DIC. Variations in isotopic fractionation between the carbon source and aquatic organic matter, commonly caused by fluctuating dissolved CO_2 concentration, may also play an important role (Street-Perrott *et al.*, 1997; Hollander and

Smith, 2001) as can input of DIC and particulate organic matter from the catchment (Boutton, 1991).

At the circumpolar forest-tundra transition, centennial- to millennial-scale changes in $\delta^{13}\text{C}_{\text{org}}$ appear to be mainly driven by changes in watershed vegetation, delivery of dissolved CO_2 from soil decomposition, and hydrology (Wolfe *et al.*, 1996; 1999; 2003; Hammarlund *et al.*, 1997). At Lake Spåime, the $\delta^{13}\text{C}_{\text{org}}$ values are relatively low during the forest phase, probably due to increased influx of ^{13}C -depleted dissolved CO_2 from soil respiration in combination with rapid hydrological flushing. Relatively low $\delta^{13}\text{C}_{\text{org}}$ values during the forest phase are consistent with $\delta^{13}\text{C}_{\text{org}}$ trends observed at several other tundra lakes in central Canada and northern Russia that have experienced episodes of increased density of forest vegetation and associated soil formation during the Holocene (Wolfe *et al.*, 1996; 1999; 2003; MacDonald *et al.*, 2004). The slight positive shift in $\delta^{13}\text{C}_{\text{org}}$ values subsequent to the forest retreat from Lake Spåime may have been caused by a reduction in the supply of soil CO_2 , as a result of declining rates of soil respiration and subsequent ^{13}C -enrichment of lakewater DIC. Indeed, the general forest retreat in the Scandes during the later part of the Holocene has commonly been associated with soil degradation and erosion (Jonasson, 1991; Snowball, 1996). A reduced supply of dissolved CO_2 from the catchment and a subsequent lowering of CO_2 concentration in the lake water may have also led to a decrease in carbon isotope fractionation between DIC and aquatic organic matter, as has been proposed in other studies (Wolfe *et al.*, 1996; 1999).

Several variables and processes may also influence the nitrogen isotope composition of organic matter ($\delta^{15}\text{N}_{\text{org}}$) in lakes (Talbot, 2001). For aquatic plants, these include the isotopic signature of available nitrogen reservoirs, nitrogen isotope fractionation and transformation in the water-column and sediments, such as

denitrification and ammonia volatilization, which lead to ^{15}N -enrichment of the residual dissolved inorganic nitrogen (DIN) pool (Teranes and Bernasconi, 2000). Strong kinetic effects can occur during nitrate and ammonium assimilation, although isotopic fractionation may be small in environments where DIN is limiting or during fixation of atmospheric N_2 by cyanobacteria (François *et al.*, 1996).

Lake sediment $\delta^{15}\text{N}_{\text{org}}$ values have also been shown to vary in association with changes in catchment terrestrial vegetation and hydrology at sites along the forest-tundra ecotone in Eurasia (Wolfe *et al.*, 1999; 2003). However, the $\delta^{15}\text{N}_{\text{org}}$ response at these sites is far more variable than $\delta^{13}\text{C}_{\text{org}}$. The stratigraphic shift to higher $\delta^{15}\text{N}_{\text{org}}$ values following deforestation at Lake Spåime is similar to Lake Yarnyshnoe-3 on the Kola Peninsula, Russia (Wolfe *et al.*, 2003), but opposite in trend to Poteryanny Zub Lake, also on the Kola Peninsula (Wolfe *et al.*, 2003), and Middendorf Lake near the lower Yenisey River, Russia (Wolfe *et al.*, 1999). The enrichment in ^{15}N following deforestation at Lake Spåime is unlikely to be related to an increase in the input of terrestrial organic matter as noted above (Figure 9). Alternatively, the ^{15}N -enrichment, as well as the elevated C/N ratio recorded at this stage, may reflect a slight decrease in nitrogen available to the aquatic plant community. Productivity-driven enrichment in ^{15}N of DIN may lead to increasing $\delta^{15}\text{N}$ values of aquatic plants (e.g., Gu *et al.*, 1996; Teranes and Bernasconi, 2000; Talbot and Lærdal, 2000; Talbot, 2001). Although many of

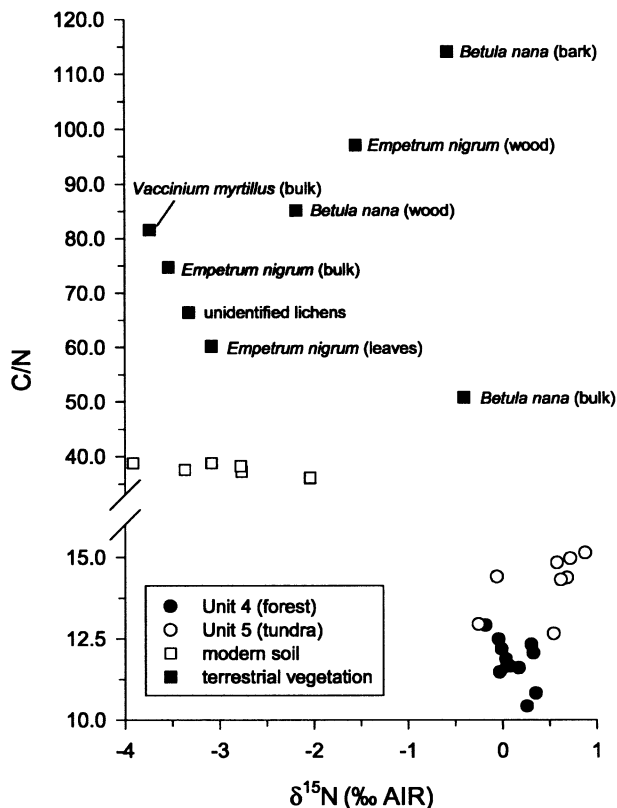


Figure 9 Crossplot of $\delta^{15}\text{N}$ versus C/N for samples of lake sediments, modern soil and terrestrial vegetation. C/N ratios for soils have been corrected for minor inorganic N content as determined by a simple TOC-TN crossplot test (cf. Talbot, 2001). No inorganic nitrogen was observed in a similar test performed on the lake sediment data. Note that the stratigraphic shift in these parameters at the deforestation of the site (Figure 5) probably does not reflect an increase in the input of terrestrial organic matter, since modern terrestrial vegetation and soil organic matter have markedly low $\delta^{15}\text{N}$ values.

these previous studies have suggested that elevated C/N ratios and $\delta^{15}\text{N}$ values may develop under conditions of increasing eutrophication, we speculate that, while total aquatic productivity declined after the forest retreat, an even greater decline in soil-derived nutrient supply may have led to a net increase in nitrogen demand by algae, possibly similar to processes that produced higher $\delta^{13}\text{C}_{\text{org}}$ values in the Lake Spåime sediment record. If DIN leached from catchment soils is indeed a limiting nutrient, the decreased efficiency of this process could be the main explanation for the drastic decline in aquatic productivity at the forest retreat around 3700 cal. BP.

General implications for the Holocene climate development in the region

The long-term Holocene descent of the altitudinal tree limit in the Scandes has been attributed primarily to decreasing growth-season temperature related to orbital forcing (Kullman, 1992; Kullman and Kjällgren, 2000). The chironomid-inferred temperature reconstruction from Lake Spåime, which can be assumed to be of regional significance for the area represented by the megafossil data sets, provides an independent basis for evaluating climatic causes of this major vegetational change. Notably, the major trends in the inferred temperature record do not differ substantially from other recently published temperature reconstructions from northern Fennoscandia based on similar palaeolimnological transfer functions (Korhola *et al.*, 2000; 2002; Seppä and Birks, 2001; 2002; Rosén *et al.*, 2001; Hammarlund *et al.*, 2002; Bigler *et al.*, 2002), with the exception of the early-Holocene temperature optimum. The latter should be interpreted with caution as it may to some extent be influenced by nonanalogous organism communities, although the WA-PLS regression technique generally performs well in nonanalogue situations (Birks, 1998).

As indicated by the temperature reconstruction (Figure 8), declining summer temperatures probably contributed to some important patterns of tree-limit change, such as the episodes of enhanced tree-limit retreat of *Pinus sylvestris* prior to 9000 cal. BP (Kullman and Kjällgren, 2000) and the general tree-limit descent around 5000 cal. BP (Kullman, 1995). However, the apparent lack of any continuous Holocene trend in the chironomid-based reconstruction of mean July air temperature suggests that other dynamics of the growth-season climate also affected the persistent tree-limit retraction and the associated changes in species composition (cf. Barnett *et al.*, 2001). The availability of moisture was probably a critical factor determining the distribution of subarctic forest ecosystems during the early Holocene, as the enhanced summer insolation at high northern latitudes at this stage led to increased evapotranspiration. Therefore, increased precipitation brought about by more frequent cyclonic activity may have characterized the early-Holocene climate along the eastern margin of the Norwegian Sea, enabling growth of *P. sylvestris* at very high altitudes (cf. Dahl and Nesje, 1996). Abundant precipitation and increased cloudiness associated with enhanced zonal atmospheric flow could thus have moderated the summer warmth that would be expected as a response to the orbital configuration. Such a scenario was recently proposed for the Abisko area, c. 600 km further north at a similar geographical setting in the Scandes, based on pollen-inferred climate reconstructions and oxygen isotope records obtained from lake sediments (Hammarlund *et al.*, 2002). The establishment of *P. sylvestris* at high altitudes shortly after deglaciation in the study area, in contrast to substantially later expansions (7000–6000 cal. BP) further north in the Scandes (Kullman, 1993b; Barnekow, 1999; Seppä *et al.*, 2002), may be related to relatively early snowmelt and prolonged growth seasons in this more southerly location.

Evidence of elevated effective moisture during the early Holocene is also provided by the available vegetational data from Lake Spåime and the surrounding area. Relatively high values of *Salix* pollen and Polyodiaceae spores prior to *c.* 9600 cal. BP suggest abundant waterlogged soils (Holmgren, 2000). The chironomid fauna around 10 000 cal. BP includes an anomalously high abundance (23%) of *Chaetocladius cf piger* (Figure 7). This taxon is often associated with running water or semi-terrestrial habitats (e.g., Wiederholm, 1983), and its abundance may reflect inwash of semi-terrestrial larvae and larval head capsules into the stream and lake, indicating enhanced surface runoff at this stage. The subsequent increase in *Alnus* pollen frequencies to maximum values around 7500 cal. BP (Figure 4), coinciding with a clear peak in the frequency of *A. incana* megafossils (Figure 8), may reflect relatively moist conditions also after the establishment of boreal forest at the site (cf. Kullman, 1995).

As a result of successively decreasing summer insolation and declining seasonality during the later part of the Holocene, high-altitude boreal forests were no longer favoured by abundant moisture supply. Instead, the regional tree limit was probably suppressed by increasing net precipitation, to a large extent through the influence of late-melting snowcover (Kullman, 1995), consistent with increased frequencies of *Salix* and Cyperaceae pollen, as well as *Sphagnum* spores during the last 3–4 millennia at Lake Spåime (Holmgren, 2000). This development led to the retreat of continuous forest from the site at *c.* 3700 cal. BP, reflected in the chironomid record as a significant shift in the species assemblage (Figure 7). The loss of trees from the lake catchment may have directly influenced chironomid taxa associated with forest and related plant macrofossils reaching the lake. In addition, the fauna was most likely indirectly affected by changes in the lacustrine nutrient regime as the continuous forest receded. As indicated by the chironomid-inferred temperature reconstruction (Figure 8), growing-season temperatures were generally high enough to support trees during the remaining part of the Holocene, especially around 2300 cal. BP, when the chironomid fauna changed significantly, most likely in response to slightly higher temperatures. However, the period from *c.* 3800 to *c.* 1000 cal BP is characterized by increased climatic variability which may have contributed to the long-term retraction of boreal forest, and prevented renewed forest dispersal during relatively warm intervals. The inferred temperature minimum around 350 cal. BP, with slightly lower values compared to present-day conditions, indicates a cooling during the 'Little Ice Age'.

The organic matter content of alpine lake sediments in southern Norway has been shown to correlate well with tree-limit dynamics as inferred from tree megafossil data (Dahl and Nesje, 1996). As demonstrated by Nesje and Dahl (2001), the most significant Holocene perturbation identified based on this approach is a decrease in aquatic productivity, the 'Finse event', possibly related to the so-called 8200 cal. BP cold event identified in Greenland ice cores (Alley *et al.*, 1997; Barber *et al.*, 1999). The Lake Spåime record is also characterized by a pronounced decrease in TOC content shortly before 8000 cal. BP, which is accompanied by changing forest composition as indicated by pollen data (cf. Tinner and Lotter, 2001) and a chironomid-inferred temperature minimum (Figure 4). The significant shift in the chironomid assemblage at *c.* 8600 may reflect a cooling as *Psectrocladius sordidellus* gr and *Tanytarsus pallidicornis* gr decrease while *Corynocera ambigua* and *Tanytarsus lugens* type increase (Figure 7). Insufficient stratigraphic resolution and chronological uncertainties (cf. Bennett, 2002) preclude a definitive correlation of these stratigraphic changes to the Greenland $\delta^{18}\text{O}$ record as well as a more detailed palaeoclimatic analysis.

However, this apparently climate-related disturbance of the lacustrine environment lends further support to the use of sediment TOC content as a rough proxy for catchment forest density in complement to macrofossil analysis.

Concluding comments

The retreat of continuous forest from the catchment of Lake Spåime occurred at *c.* 3700 cal. BP, during an episode of pronounced cooling and/or increased humidity as suggested by numerous proxy records from northwestern Europe (Anderson *et al.*, 1998; Snowball *et al.*, 1999; Nesje *et al.*, 2001; Seppä *et al.*, 2002; Hammarlund *et al.*, 2003). The lack of firm evidence for declining summer temperatures in northern Scandinavia at this stage (e.g., Rosén *et al.*, 2001; Seppä and Birks, 2001; Calvo *et al.*, 2002; Korhola *et al.*, 2002; this study) suggests that increasing humidity was the decisive mechanism. Increased climatic variability during the later part of the Holocene may have contributed to the general lowering of alpine tree limits. Submillennial-scale climate dynamics responsible for the assumed increase in effective moisture may thus have amplified the altitudinal retraction of boreal forest in the Scandes. However, the long-term Holocene trend was probably related to a combination of decreasing growth-season temperature, declining seasonality and strong zonal atmospheric flow across northern Scandinavia during the early Holocene, all processes brought about by orbital forcing (Hammarlund *et al.*, 2002; Seppä and Birks, 2002). More detailed palaeoecological relationships, such as the changing species composition and density of the former high-altitude forests, cannot be assessed based on the available stratigraphic data. The possible response of local environmental conditions to large-scale atmospheric circulation dynamics will be explored based on additional vegetational records and studies of isotope palaeoclimate by means of oxygen isotope analysis of aquatic cellulose from lakes in the area.

The forest retreat was accompanied by declining aquatic productivity as reflected by lowered carbon and nitrogen contents of the sediments. The decreased productivity was probably induced by a reduction in nutrient supply from catchment soils, evidenced by increased C/N ratio and enrichment in ^{13}C and ^{15}N of lacustrine organic matter. Apparent variability in the response of these parameters to vegetation and climate change in different settings indicates that changes in nitrogen dynamics are site-specific and, thus, it is currently difficult to predict possible nitrogen cycling responses to future changes in climate and vegetation at this ecotonal boundary. On the other hand, the remarkable consistency of lake sediment carbon isotope response to past increases in forest vegetation at several locations near the circumpolar forest-tundra transition suggests that an important positive climate feedback mechanism may develop from additional CO_2 flux to the atmosphere via release from lake waters in response to future warming. This process could become active if aquatic productivity is unable to keep pace with the export of dissolved CO_2 from catchment soils related to potential future episodes of tree-limit advance and ascent (Wolfe *et al.*, 1999; cf. House *et al.*, 2002; MacDonald *et al.*, 2004).

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